ADVANCES IN THE ECOLOGY OF LAKE KARIBA

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Cover Top: Typical ringnets as utilized in Kapenta fisheries on Lake Kariba
Bottom: Lake Kariba: The littoral area and draw-down zone
Back cover: Lake Kariba: The ecology of the littoral area is strongly influenced by wildlife.

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INTRODUCTION

Jacques Moreau

Lake Kariba (16° 28' to 18° 06' S; 26° 40' to 29° 03' E) (Figures 1 and 2) was formed by damming the Zambezi River at the Kariba Gorge, between 1955 and 1958, and it became filled in 1963. It is the third largest man-made lake today with an area of 5 364 km^2, at 485 m. a.s.l., a length of 277 km and a mean depth of 29 m (maximum 120 m) (Balon and Coche 1974).

A number of ecological characteristics make this tropical man made lake fairly unique compared with the other great lakes on the African continent. The mean retention time of the waters is only about 3–4 years and the bulk of the water is lost through hydro-electricity turbines. Being in a tropical area with seasonal rainfalls, the lake experiences annual draw-downs of about 3 m although this is exceeded during periods of drought. Lake Kariba lies over an infertile bedrock and the overall productivity is dependent on nutrient inflow from the catchment (Marshall 1982), so that productivity declines in periods of drought.

The Zambezi River contributes about 70% of the water inflow. Next in importance is the Sanyati river which discharges into the lake close to the dam (Figure 2). Also the wide seasonal fluctuations in water temperature (between 20 and 30°C) at the surface and the monomictic turn-over in July-August, with a period of maximum stability between December and April, are important in relation to seasonal fluctuations in productivity.

These factors and others combine to give the lake some specific ecological characteristics. For example, the draw-downs create unstable littoral habitats which can only be colonized by few benthic organisms with broad tolerance limits (Machena 1989). On the contrary, the alternations in flooding and drying along the stretches of gently sloping shorelines with the subsequent growing and decomposing of ephemeral vegetation are a source of nutrients and a favourable environment for growth and reproduction of some fish species, particularly tilapiine fishes, during inundations (Donnelly 1969, McLachlan 1970).

Before the Zambezi River was dammed, the Gwembe valley, where Lake Kariba is now situated, was described as woodland and, in the driest part, thicket vegetation (Child 1968). Along the river was a fringe of evergreen riparian forest and seasonally inundated grassy floodplain, where the valley was wide. The area had a sparse human population and abundant game populations in zones far from human habitations (Child 1968). Before impoundment, the most important fish in the Zambezi River were typical riverine species, notably cyprinids, distichotontids and characids. Small species were rather scarce due to little cover in the sand-bank river and heavy predation from the tigerfish, *Hydrocynus vittatus*, (Jackson 1961). Larger cichlids were also uncommon (Marshall *et al.* 1982).

With the creation of the lake, the most fertile parts of the valley, i.e. the riparian forests and the floodplains, largely on alluvial soils, became flooded. The new shoreline consisted of the comparatively infertile hillsides. In some places,

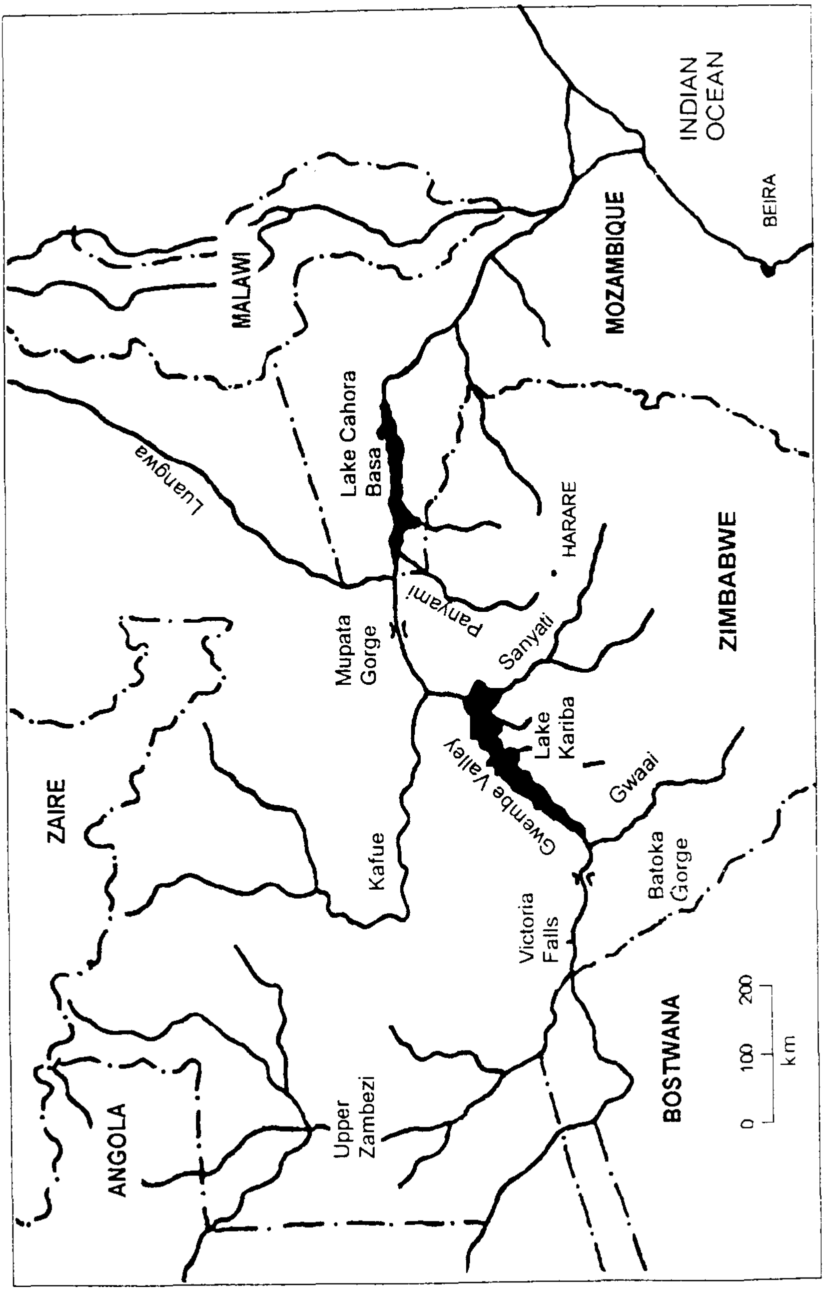

Figure 1 The Zambezi catchment area with location of Lake Kariba

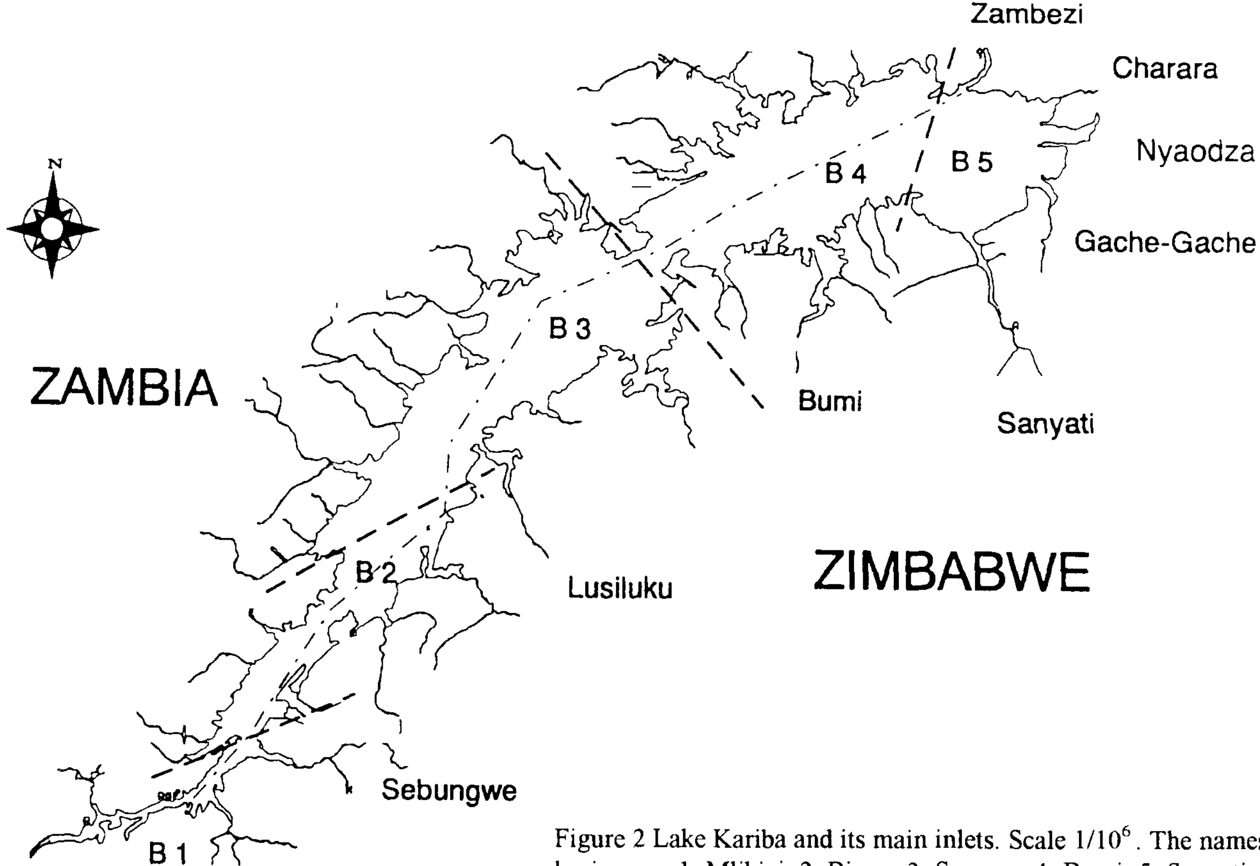

Figure 2 Lake Kariba and its main inlets. Scale $1/10^6$. The names of the basins are: 1: Mlibizi; 2: Binga; 3: Sengwa; 4: Bumi; 5: Sanyati

(about 20% of the area of the lake) trees were cut before the reservoir was filled in order to facilitate fishing operations, but in most places trees were left standing.

After the lake was formed, it has undergone changes in its physico-chemical characteristics and a marked succession in plant and animal development occurred (Coche 1968, Magadza 1970, McLachlan 1969, McLachlan and McLachlan 1971, Balon and Coche 1974, Balon 1978, Marshall and Junor 1981, Machena and Kautsky 1988, Machena 1989).

In the early filling phase, nutrient leakage from the flooded terrestrial habitats was high; total dissolved solids (TDS) rose from 55 mg l^{-} (in the former Zambezi River) to 65 mg l^{-1} in the lake by 1960. Initially, The nutrient load and the rising lake waters enabled high reproduction, survival and growth of fishes. However, the high catches recorded in the early sixties in the inshore fisheries declined steadily from 1965 as the nutrient level decreased following massive loss of nutrient through hydro electric turbines and stabilized around 1973 (Balon 1978).

There was also an explosive growth of the floating fern *Salvinia molesta* which covered 22% of the lake in 1962 and probably locked up large quantities of nutrients (Mitchell 1973). From around 1972, it shrank considerably (Marshall and Junor 1981) and is now practically absent.

Fish population changes have also been marked since the lake was created (Donnelly 1970, 1972, Kenmuir 1984). Cichlid populations have increased with the establishment of a lacustrine environment and, at the same time, populations of cyprinids and distichodontids have decreased (Marshall 1984). The changes from riverine to lacustrine conditions has also produced new kinds of habitats to which the Zambezi fish were not adapted. Particularly the open pelagic region more than 15 m deep (ca 70% of the lake area) was not utilized before the introduction of the small pelagic clupeid *Limnothrissa miodon* from Lake Tanganyka in 1967–1968 (Welcomme 1981, 1988). Today, this species is the most important commercially with an annual catch of about 25,000 tonnes (Crul and Roest 1995).

About 40 species are known from the lake (Bell Cross and Minshull 1988) of which about 20 are very common. The pelagic fishery is fairly industrialized, whereas the inshore demersal species are cropped by artisan fishermen who use gillnets which are seldom set in waters more than 10 metres deep. Lake Kariba is also a holiday resort and supports a popular recreational fishery.

The aims of this general introduction are

- To briefly review the main hydrological characteristics of Lake Kariba which should be known for a proper understanding of the various contributions,
- To make the reader aware of the SAREC/UZ Project and the general context in which it took place,
- To introduce the various contributions and their linkage in the framework of a multidisciplinary approach of the ecology of Lake Kariba.

MAIN HYDROLOGICAL CHARACTERISTICS OF LAKE KARIBA

The hydrological gradient

Lake Kariba has five basins which are separated by narrows and chains of islands (Figure 2)

Basins 1 and 2 are small and narrow, and the Zambezi River which contributes 70% of the inflow, has a large influence in these areas. For six months of the year (November-May), the period in which the Zambezi is at peak flow, Basins 1 and 2 have riverine characteristics (Coche 1968). For most of this time, these basins are turbid from flood waters. By July, with the recession of the floods, the influence of the river decreases and both basins assume lake-like characteristics.

Basins 3–5 are lacustrine all-year-round. As the Zambezi River passes through the extensive Chobe swamps above the Victoria Falls, sedimentation takes place so that by the time the waters reach the lake, much of the nutrients have already been removed.

The morphology of the lake, together with the riverine influence of the Zambezi River create a hydrological gradient along the longitudinal axis of the lake, with light penetration and productivity increasing down the lake (Begg 1970).

Lake shore types

The shore line is complex and there are gentle and steep slopes as well as sheltered and exposed shores.

Extensive parts of the lake margins are occupied by steep rocky exposed shores where wave action has removed the fine material from between the rocks. These shores offer little substrate for higher plant growth. When exposed to the wind, they have a well-defined wave-cut. Below this wave-cut, there is a sloping terrace on which substratum material washed from wave-battered shores is sorted directionally. Coarse material (boulders, pebbles etc.) is left near the shore and fine material is deposited in deeper water where the back current is weak. In some cases, the boulders and pebbles extend over some distance into the water where they are replaced by sand.

Sheltered and gently sloping shores are protected from the battering effect of waves; here the shore is not scoured and deposition of fine sediments may take place. These shores are largely sandy, as the wave erosion has carried away finer material and often deposited it just below the sandy beaches.

Depth and associated gradients

Depth expresses a complex gradient, because it is correlated with a number of other gradients. There is a gradient in particle size of the substratum, with fine material in deeper water. In association with this gradient, a nutrient gradient is developed. The finer sediments are richer in nutrients, so that nutrient levels increase with depth (Spence 1982). Lindmark (this volume) found that in Lake Kariba sediments from steep slopes had a high dry weight (i.e. high proportion of sand) and a low content of organic matter whereas, at a water depth of more than 2 m, organic matter in sediments increased to 8-10% of the dry weight.

McLachlan and McLachlan (1971) also found low organic carbon and low total nitrogen on wave washed shores in Lake Kariba in comparison to sediments from deeper water and protected shores.

Light penetration decreases and the light quality changes with depth. However this may not always be the case. There is usually a band of turbid water close to the shores resulting from wave effect so that close to the shore light penetration could be low. Offshore from this turbid belt, light penetration increases and then decreases again with increasing depth.

The morphology of the lake thus has a bearing on the type of shores that result, and on the nature and type of vegetation that will colonize these bottoms and on the associated animal life.

Lake level fluctuations

The lake experiences a mean annual drawdown of 3 m (vertical range), between 487 and 483 m a. s. l. (Figure 3) because water is lost through the hydro-electric power turbines all year round and fills the lake from river floods during the summer rains. In the early filling phase of the lake, annual fluctuations were larger.

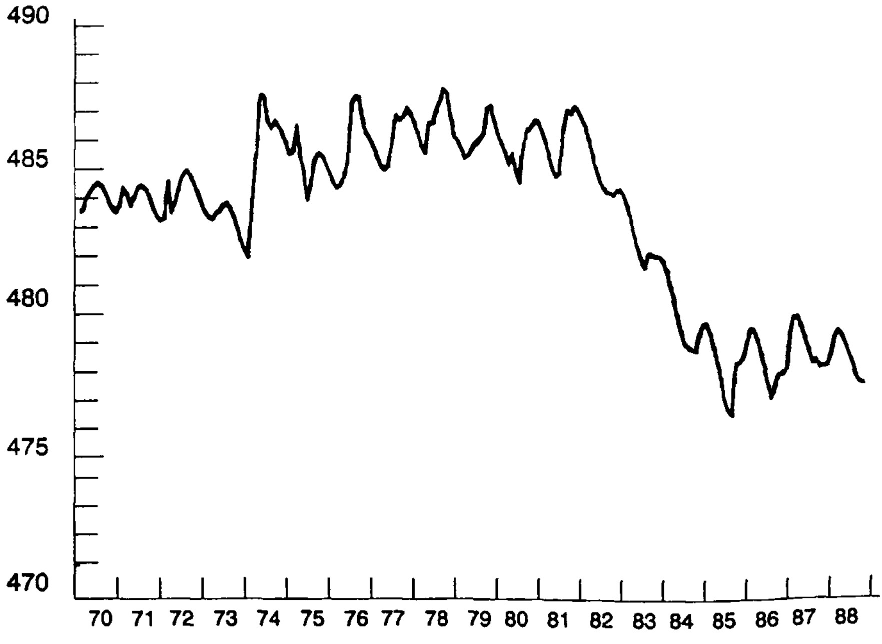

Figure 3 Water levels of Lake Kariba (m. a. s. l.) recorded at the dam wall. The recent drought began in 1980.

In periods of severe drought, the lake level falls a great deal. During the 1981–1984 drought, the lake level dropped rapidly. The locally good rains in early 1985 only partly restored the water level and in 1985, the level dropped to 476.5 m a. s.

l. , which was the lowest recorded level (Surell 1987). In 1992, the level was more than 9 m below normal. The corresponding level and surface areas of the lake are provided on Table 1:

Table 1 Lake Kariba: Estimates for surface areas and capacities at various water levels (Balon and Coche 1974)

Water level m a.s.l.	*Lake surface area sq. km*	*Lake volume cu. km*	*Hydroelectric scheme*
489	5820	178.0	Max. flood storage
488	5630	170.4	–
485	5364	156.5	Normal operating level
482	5000	141.3	–
479	4660	124.1	–
476	4325	108.2	Lowest draw-down

Physical and chemical characteristics

The physical and chemical characteristics of Lake Kariba were extensively investigated mostly by Balon and Coche (1974). The evolution of the limnological characteristics of the lake along its longitudinal axis has to be particularly emphazised as well as the clear seasonal variations of the various parameters which are closely related to the hydrology of the Zambezi River and to the climate in the whole drainage basin of Lake Kariba.

For instance, the thermal cycle in the open waters of Lake Kariba is well understood, having been described by a number of workers (e.g. Harding 1964 and 1966, Coche 1968 and 1974, Begg 1970 and 1974). The lake is monomictic, being stratified from about August until May when overturn takes place and it becomes isothermal. During the period of stratification the epilimnion and hypolimnion are separated by the thermocline which varies in depth from about 10 to 20 m. The hypolimnion was generally deoxygenated in the early years of the lake when it was still relatively eutrophic. Hydrogen sulphide was present in large quantities below the thermocline at this time. This changed as the lake matured and became oligotrophic and the extent of deoxygenation is now less severe and hydrogen sulphide is rarely encountered. The nutrients that are retained in the hypolimnion during stratification are released at overturn and become available to organisms in the upper layers.

The information available from Balon and Coche (1974) are summarized on Table 2.

THE SAREC/U.Z. PROJECT

In 1981, the University of Zimbabwe identified the Lake Kariba basin as an area where it could undertake research work leading to a direct interphase between University research activity and community needs in various disciplines. Among various tasks, the ecology of Lake Kariba was identified as an area where the University could contribute to the development effort by providing essential data relevant to the management of natural resources of Lake Kariba. The following problem areas were regarded as of particular importance:

- The evolution of the lake in time;
- The function of the pelagic ecosystem with focus on *Limnothrissa miodon* and the reason of variations of yields;
- The relation between the primary production and the fish production (can the mainly riverine fauna in the littoral zone efficiently utilize the primary production or can it be improved by introducing further species from other African lakes);
- How do the large water fluctuations affect the nutrient flow and production on the grass land and in the littoral region (Can an optimal water regulation be designed that could take into account the multiple uses of the lake: generation of electric power, agriculture, irrigation, aquaculture, wildlife, tourism and recreation?);
- The mussel resource (can it be utilised directly or can the nutrients be regenerated by introducing mussel-eating fish?);
- The competition between fishermen, fish-eating birds and crocodiles.

Table 2 General characteristics of Lake Kariba (Coche 1974)

Parameter	*Range*	*Observation*
Temperature	17–32 °C	Warm monomictic lake; homothermy in June–July (20– 22°C) thermal stratification October– June
Depth of mixed layer	15–25 m	See above
Transparency	50–1060 cm	(Secchi disk) increases from basin 1 to 5
Depth of eutrophic zone	2–24 m	Most often 10–16 m.
pH	6.8– 8.9	
Dissolved O2	6–10 mg l^{-1}	In superficial waters. Oxygen stratification from October to June
Conductivity	50–115.µmhos (k20)	
Total solids	40–70 mg l^{-1}	
Ionic content:		
Na+	1.8–4.7 mg l^{-1}	
K +	0.6–1.8 mg l^{-1}	
Ca ++	2.0–13 mg l^{-1}	
Mg ++	0.5–3.0 mg l^{-1}	
Cl-	1.0–3.0 mg l^{-1}	
NO2 -	trace	
NO3 -	0.01– 0.05 mg l^{-1}	
PO4 —	0.01– 0.05 mg l^{-1}	

The present **Ecology of Lake Kariba Research Project** resulted from a proposal submitted by the University of Zimbabwe (University Lake Kariba Research Station) to the Swedish Agency for Research and Cooperation (SAREC) in persuance of the general bilateral agreement entered into between the Government of the Republic of Zimbabwe and that of Sweden.

This project proposal was firstly submitted on 4 October 1983 and further applications were made on 3 September 1985 and on 5 December 1986 for two successive extensions. In total, it has been a 5 years-research project (1985–1989). The main objectives of the project were expressed as follows:

- To provide data for the proper utilisation and management of the diverse lake resources;
- To start to analyse the possibilities to increase the useful production from the lake;
- To train post-graduate students from U.Z. for PhD degrees in biology in order to help Zimbabwe to be self-supporting with hydrobiologists;
- To provide equipment for the limnological laboratory at the University Lake Kariba Research Station.

The project comprised of experienced scientists from four Swedish universities and from the U.Z. working in close cooperation. In addition, graduate students from the U.Z. had to participate by doing their PhD work on Lake Kariba, receiving part of their training in Sweden and supervised jointly by Zimbabwean and Swedish scientists.

In order to finalize the main results of the project, the U.Z. and SAREC jointly organized a workshop on Lake Kariba Ecology (Kariba, December 1992) during which the publication of the present book was decided and the chief editor was subsequently appointed by U.Z.

THE ORGANIZATION OF THIS BOOK

This book assembles contributions of several authors who were engaged in the SAREC/UZ Research Project in various ways.

The first chapter is a review of the dynamics of nutrients both in the lake and sediments and chemical interactions between the water column and the bottom. Chapter 2 gives the main results of a research project on nitrogen fixation which was the first of its kind in tropical Africa. The evolution of the limnochemistry of the lake is a key issue for a proper understanding of the evolution of phytoplankton and pelagic primary production during the eighties (Chapter 3).

The evolution and dynamics of zooplankton (Chapter 4) is reviewed in relationship with the evolution of climate and its influence on the chemistry, primary production and trophic status of the water but also with the development of the pelagic population of *Limnothrissa miodon*.

During the eighties, the lake experienced severe drought periods (see above) the influence of which on the plant and animal life on the shore is analysed. Chapter 5 deals more specifically with the ecology of the draw-down zone whereas Chapters 6 and 7 provide reviews of the simultaneous evolution of both littoral aquatic vegetation and associated invertebrate fauna, two groups of major importance for the general ecology of the lake.

A research was also implemented on the impact of fish predation by crocodiles (Chapter 8) and birds (Chapter 9), a subject which has been scarcely investigated in tropical Africa despite its possible importance for littoral fisheries management.

The final chapter (Chapter 10) summarizes the quantitative results of the previous chapters in terms of transfers of biomass, among the most important groups of living organisms in Lake Kariba. The background of this chapter is a preliminary study by Machena *et al.* (1993) on the trophic relationships in Lake Kariba using the ECOPATH model and software (Christensen and Pauly 1992). This chapter tends to illustrate the usefulness of a multi-disciplinary approach of the whole lake by specialists of various groups and disciplines for a proper understanding of the overall ecology of Lake Kariba.

The final conclusion deals with some managment issues and stresses the need of further research in order to fill some gaps in our present knowledge of Lake Kariba ecology.

ADVANCES IN THE ECOLOGY OF LAKE KARIBA

This book assembles contributions of several authors engaged in the SAREC/UZ Project on the Ecology of Lake Kariba. Various problems, regarded as particularly important, are dealt with, for instance:

- The evolution of the lake in time;
- The function of the pelagic ecosystem with focus on *Limnothrissa miodon* and the reason of variations of yields;
- The relations between the primary production and the fish production in the littoral area;
- The possible impact the large water level fluctuations on the nutrient flow and production on the grass land and in the littoral region;
- The utilisation of the mussel resource;
- The competition between fishermen, fish-eating birds and crocodiles.

This is an essential reading for students, academics and environment managers interested in tropical aquatic ecology in Zimbabwe and in the rest of the world.

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